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ABSTRACT

In an attempt to accommodate each of two perspectives (nature versus nurture) in the formulation of a developmental framework, two complementary approaches to developmental theory are presented. First, consideration is given to what is now known about the developmental process in general (thought out in terms of the question "Where is the information for development?"). It is concluded that the genome and the environment must interact in development. Furthermore, the environment is best thought of as having a constructive role in the developmental process. The biologically oriented theory of probabilistic epigenesis proves to best accommodate these conclusions. It is argued that this "development from" perspective fails to adequately account for the "central tendencies" of the genome, consideration of which is central to the "development to" perspective in biological and evolutionary thought. Maintaining an interactionist position, the paper concludes that development to an evolutionarily adaptive endstate is environment-expectant. The notion of conditional probabilities in development is presented. Four qualitatively different types of environmental conditions that may be involved in development to species-typical endstates are delineated. (BW)

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TWO BIOLOGICAL PERSPECTIVES ON SPECIES-TYPICAL DEVELOPMENT

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TABLE OF CONTENTS

Introduction and Overview.....1

Conceptions of Gene and Environment.....6

The "Development From" Perspective.....11

Where is the information for development?.....12

The environment: Constructive or permissive?.....19

Probabilistic epigenesis.....23

The "Development To" Perspective.....30

The genome as a blueprint for development.....32

The central tendencies of the genome examined.....34

Conditional probabilities.....39

Four categories of environmental factors.....42

Conditional probabilities in the development of birdsong.....46

Advantages of the conditional probabilities model.....55

Normal, natural, and universal.....56

Innate and experiential -- the semantics of nature-nurture....59

Summary and Implications for Potential.....65

INTRODUCTION AND OVERVIEW

At the height of a heated debate over the roles of nature and nurture in development, two Berkeley scientists point to a pair of sparrows singing in a nearby tree, and each insists, "There! Those sparrows prove my point." (The sparrows, one a white-crowned sparrow and the other a song sparrow, are both native to the Berkeley area and are singing quite different, species-typical songs.) The first scientist points out that these two birds have grown up in essentially the same environment -- same weather, same food choices, same temperature, they may have even been reared in neighboring trees hearing the same songs -- yet the songs that they do sing are readily distinguishable. Furthermore, claims the first scientist, the two birds could be raised in rigorously identical laboratory environments yet the songs would still differ. Clearly the differences between the birds must be genetically determined. The second scientist objects, having read that white-crowned sparrows *learn* their species-specific song; in fact, the sparrow will sing the regional dialect of song that he heard as a fledgling for the rest of his life. Moreover, if the young white-crowned sparrow is deafened, his song will develop in a highly abnormal manner. Thus, not only does the sparrow imitate an adult song model that he has heard early in life, but he must also hear his own voice feed back as he learns to sing. Clearly, claims the second scientist, sparrow song must be environmentally determined.

Both scientists' conclusions seem sound; yet, logically, they seem

at the same time mutually exclusive. The classic solution to this bind in the history of the nature-nurture debate has been to ask which is *more* important, gene or environment, in the development of song. I will argue in this paper that the two conclusions are, upon closer examination, not at all incompatible, and that development is in fact understood best by considering both genome *and* environment, rather than by attempting to emphasize exclusively one or the other. In the course of this argument it will become necessary to revisit distinctions which have been widely bandied about in the past, like genetic vs. environmental determination, but it will also prove necessary to introduce distinctions that have not been so widely recognized.

There are many pieces to the puzzle of constructing a coherent and consistent viewpoint of the influences of genome and environment on development. Such a viewpoint must treat with equal consistency species that learn and species that do not, species whose phenotypes are very rigidly defined and those that are more variable. The arguments presented here lead toward such a simple and coherent view; the path, however, that must be walked to arrive at this view is unavoidably complex and somewhat tortuous. In the interest of aiding the reader in following the logic and structure of these arguments, the completed puzzle is mapped out in Table 1, which outlines both the relevant questions posed in the course of this discussion and how the answers offered influence both the direction and the nature of the ensuing argument. Let me briefly trace the structure of the argument.

Take the case of birdsong as an example. Generally, the two scientists'

Table 1.

Field of Developmental Sciences

Playground for the Nature-Nurture Debate

Biological Issues

"DEVELOPMENT FROM" PERSPECTIVE

Basic question asked is one central to the nature-nurture question: Where is the information for development? What controls/directs the process? How?

↓

Answer is found in the relationship between the genes and the environment.

↓

The question arises: What is the role of the environment? Does it permit genetically-determined endstates to develop or does it construct endstates?

↓

What theory of development can account for the conclusions reached? Predetermined vs. probabilistic epigenesis are two choices.

"DEVELOPMENT TO" PERSPECTIVE

Perspective arises out of the view that development seems to proceed toward adaptive endstates -- the genome seems to have some "central tendencies." Use of the shorthand of the genome as a "blueprint" for development to account for "development to."

↓

This shorthand can be -- and often is -- construed to imply that the endstate is genetically determined.

↓

New shorthand of conditional probabilities is presented since development to an adaptive endstate is environment-expectant.

↓

Four categories of environmental conditions are explicated.

↓

Semantics of Nature-Nurture

What do we mean by gene and environment?	"Strength" words denoting which factor has the greatest role in guiding development: inherited, innate, learned, experiential.

argument over birdsong falls within the realm of the field of development, a field composed of many areas of controversy and multiple disciplinary perspectives on such issues. A prime discipline to target in the nature-nurture debate is biology, where genetic and environmental influences on development have been studied most directly. But here is where the complications start. The two scientists may have come to such disparate conclusions about the nature of the genetic and environmental influences on birdsong development because their interests in the problem and the perspectives that they bring to bear on it are very different. Indeed, at least two distinct perspectives on development presently exist in biology (Lehrman, 1970). Some biologists are primarily concerned with *development from* any state in development, and in the processes that are going on at that time; others are more interested in *development to* a certain endstate, and in how the developmental processes lead toward that endstate. Lehrman (1970) summarizes:

> One way of putting this point is that the student of adaptation and evolutionary variation often regards development as proceeding, at any stage, *toward* the functional form, since it is the functional form that is adaptive and since natural selection has acted to select genomes which, in a natural environment, produce the functional form; while for the analytic student of ontogeny, development must be seen as proceeding, at any stage, *out of* the immediately preceeding stage, and as being produced by processes going on at that time, since it is *his* aim to understand the processes that create developmental change.

Let me elaborate on this further.

The "analytic student of ontogeny" is the developmental biologist -- the embryologist, the developmental geneticist or neurobiologist or endocrinologist -- who has as his[1] goal an understanding of how the processes of development work. He emphasizes *ontogeny* over endstates.

---

[1] "He" will be used throughout this paper in the generic sense to be interchangable with "she."

A developmentalist examining birdsong might be inclined to take the perspective of our second scientist, and ask such questions as: What are the conditions that are necessary for development? How do physical processes control this change? If the conditions of development are manipulated, does the altered process produce different endstates? Through exploring these questions, he hopes to better understand *how* vocal feedback and imitation of an adult song model contribute to song development -- how these events affect the development of the brain, hormonal production, even genetic activity.

With respect to the nature-nurture debate, though, the task of the developmental biologist is more limited. He can explore at least one question that is central to the debate: Where is the information for development? Somewhere must be the information responsible for the workings of the developmental process -- it may be in the organism's genetic constitution, or it may be in the environment, or in both. In many cases, including the white-crowned sparrow, environmental experience obviously contributes to development. Thus, since the nature-nurture debate centers on the issue of which is primarily responsible for development, genome or environment, a crucial question emerges: Is the essence of the developmental outcome specified by the genome of the organism, and do the environmental events that facilitate development simply allow the genetic plan to unfold? Or must the environment be granted a more constructive role in building outcomes and be given equal consideration with the genome it terms of being a source of information (in *all* cases, not just those in which learning can be clearly demonstrated)? If the "development from" perspective can supply an answer to the question, "Where is the information for development?", we will be much better equipped to examine the roles of genome and environment in development.

The "development to" perspective, on the other hand, is most readily characterized by the ethologist, a biologist who studies behavior from an evolutionary perspective, and by other evolutionary biologists. The ethologist may be interested in the adaptiveness of an organism's behavior in its natural state -- how behavior facilitates survival and reproduction. It is apparent, especially to those who study the adaptiveness of functional endstates, that the development of organisms in a natural setting is directed toward the attainment of that endstate. Birdsong, for example, plays a crucial role in the maintenance of a male's territory and his attraction of a mate. In many bird species, there seem to be strong "central tendencies" for individuals to develop this complex behavior: the neural circuitry underlying song has been well-worked out, and is present (though developed to less a degree) even in females in species where the female does not sing.

The ethologist, the evolutionary scientist, or the sociobiologist often desires a shorthand method of addressing the complex mechanisms of development which lead to such adaptive endstates. (Recall the perspective of the developmentalist, and the host of minute genetic, hormonal, and neurological details entailed in a full consideration of the process. For many, a shorthand is a necessary alternative to the "how" details.) Commonly, the shorthand has consisted of the metaphor of the genome as a "blueprint" for development. Through this metaphor, one can account for the development of song in the white-crowned sparrow as a product of genetically-guided maturation of the song control areas of the brain, coupled with genetically-prepared learning of adult song models. It is likely that the first scientist in the opening argument over birdsong was taking this perspective,

arguing that the difference in the genetic blueprints of the white-crowned and song sparrows resulted in their differing developmental outcomes.

As is demonctrated from the example of birdsong, the ethologist and the developmentalist may not be studying different problems, but rather are bringing different and valuable perspectives to bear on the same problems. It must, however, be the goal of any comprehensive developmental science to account for both aspects of development, development from a preceeding state and development to a functional form. Only such a science will prove satisfactory to both those concerned with the adaptiveness of the endstates of development and those concerned with the workings of the developmental process itself. Unfortunately, the conclusions reached from the "development from" perspective in this paper will prove not altogether compatible with the "development to" shorthand of the genetic blueprint described above. Most of the section on the "development to" perspective is an attempt to describe this problem and to introduce a solution to it.

In an attempt to accommodate each of the two perspectives in the formulation of a developmental framework, I present in this paper two complementary approaches to developmental theory. First, I consider what is now known about the developmental process in general (thought out in terms of the question "Where is the information for development?"), and conclude that the genome and the environment must interact in development; furthermore, the environment is best thought of as having a constructive role in the process. The biologically-oriented theory

of probabilistic epigenesis proves to best accommodate these conclusions. I will then argue that, at least at this point in time, this "development from" perspective fails to adequately account for the "central tendencies" of the genome, consideration of which is central to the "development to" perspective in biological and evolutionary thought. Rather than falling back on the traditional, genetically-oriented explanation of this phenomenon, I attempt to remain true to an interactionist position. I conclude that development to an evolutionarily-adaptive endstate is environment-expectant, and present the notion of conditional probabilities in development, a modification of the "genome as blueprint" metaphor. I also will delineate four qualitatively different types of environmental conditions that may be involved in development to species-typical endstates.

Entrenched in this discussion are the terms that are constantly bandied about in the nature-nurture debate: genetic, environmental, innate, learned, inherited, experiential. The first two, gene and environment, can be discussed in a fairly straightforward manner, and I will do so in the following section as a necessary preliminary to the bulk of this paper. The latter terms, however, are commonly used to denote the "strength" of genetic or environmental influences on development -- which is "more" important, gene or environment? As such, a fruitful discussion of these semantics must be postponed until after completing the discussion of to where the "from" and "to" perspectives lead.

When Darwin first formulated his theory of evolution, he had no real notion of what the carrier of hereditary information would turn out to be. It was not until Mendel that discrete units of heredity were termed "genes." Avery discovered, and Hershey later confirmed, that deoxyribonucleic acid (and not protein) was transmitting the genetic information, and Watson and Crick only about thirty years ago offered evidence of a structure of DNA which would permit its exact sequence to be preserved during replication. Now, through extensive work in molecular genetics, we have a concept of the gene as a double-stranded helix of DNA that replicates, randomly mutates, and is transcribed into RNA, which is in turn translated into the proteins which do the work of the cell. Unfortunately, we have no similarly exact conception of what it is that we're talking about when we say "the environment."

First, it is not at all clear at what level the environment is best dealt with, or if the choice of a level is arbitrary. Take, for example, the case of several scientists studying the influence of the environment on the development of song in the white-crowned sparrow. The geneticist on the case might opt to deal with the cell as the relevant level of the environment: for the DNA molecule itself, the chemistry of the medium which surrounds it bears the most relevance to whether and in what form the information in the DNA will be expressed. The embryologist, however, may consider not the cell but the sparrow egg as the relevant environment. In emphasizing environmental influ-

ences on the development of the embryo to the fledgling, the embryologist may be primarily concerned with how the chorionic and amnionic environments provide the embryo with nutrients and oxygen and remove waste, or with how embryonic behavior affects the newly hatched fledgling's behavior. Finally, the ethologist on the sparrow case may view the environment relevant to the development of the bird's song in adulthood as the species community (or culture, to strain the term). He concentrates primarily on how, for example, the organism is affected by hearing conspecific song at certain points in its development. The ethologist with a neurobiological bent may even switch levels of analysis as his work progresses, becoming more of a developmentalist: he might consider the effect of hearing song on gross neural development (the interface with the environment being at the whole brain level of physiological processing of sensory input) or even the effect of exposure to song on the activity of the DNA itself (the interface being, as with the geneticist, at the level of the functioning single cell).

From a reductionist standpoint, the ultimate level of studying the environment appears to be at the level of the cellular biochemistry. More commonly, and more practically in most cases, the environment is considered not in terms of the cell -- these changes are assumed -- but as being all of the things external to the organism (like culture, food, or radiation). It is not clear whether there is a single level of analysis which is more appropriate than any other for every kind of inquiry. It could, for example, be argued that the most obvious candidate, the cell, is an inappropriate level since the DNA in essence has "created" its own environment in the cell. If this is true,

however, can it not also be argued that the DNA has further created the organism to house the cell, and the culture to house the organism? Rather than to adopt this approach or any other which limits the scope of the term "environment" *a priori*, it seems at present more useful to concede the potential validity of any of these levels of analysis, and leave to the future the determination of whether one level does eventually supercede all others in its power of explanation.

Suppose, though, that we did know all the levels at which the effects of the environment are appropriately studied. Even so, it is possible, even probable, that we presently lack a language designed to appropriately describe the environment. A developmental science which considers both gene and environment must naturally attempt to describe lawful relationships between the two. For example, our ethologist might posit that when a male white-crowned sparrow hears conspecific song during the first weeks of life, neural development in the song-produucing areas of the brain is stimulated. He has thus laid out a lawful relationship between conspecific song and later neural development. (Presumably changes in genetic activity are involved in the mediation of the latter.) However, the question appears: What is it about "song" that stimulates the development? What properties of song are contributing to development, and how? Fodor (1980a) describes the catch as, "What this comes down to is that, at a minimum, '*x*'s being F causally explains . . .' can be true only when 'F' expresses nomologically necessary properties of the *x*s." Translated into our example, "birdsong's being F causally explains subsequent neural development" can be true only if the ethologist

posits an 'F' which is some lawful property of birdsong, i.e., one of its physical properties. And having a language that describes the phsyical properties of environmental objects, like salt being NaCl, depends very much on the state of the arts in chemistry and physics.

Using a physically-based descriptive language rules out the following types of explanations of development:

(1) Conspecific song, being what stimulates neural development in a sparrow, stimulates neural development in the sparrow.

(2) Conspecific song, being conspecific song, stimulates neural development in the sparrow.

But, one might ask, what is wrong with the latter explanation? What is the difference between "Conspecific song" and what "conspecific song" refers to? Fodor (1980a) presents a philosophical answer to this question, to which the reader of a philophical bent is referred. I think it perhaps simpler to note that if one has some way of saying what the song is physically, the path is open to explore which of these properties determine the causal relationship between song and development, and what physical development events occur as a result of stimulation.

Luckily (and conveniently for this discussion), the ethologist has indeed developed a language of reference to the properties of song: sound spectrographs reveal that each song is characterized by vocalizations of certain frequencies and durations which form a species-specific pattern (although local "dialects" and individual variations do exist). Research is currently being undertaken to determine which properties of song are sufficient for the song to be

recognized as species-specific. Many other areas of biological inquiry into the developmental process are similarly grounded in physical or chemical terms; nutritional intake, temperature, and visual input are a few examples of environmental factors that are strongly rooted in the terminology of chemistry and physics.

This kind of descriptive language is apparently well-suited to biological developmental research. Other, nonbiologically-oriented areas of developmental science are not, however, based in these terms, nor is it clear that they should be. Certainly in human development, the expectations of others are part of the child's environment; I doubt, though, that a chemist will ever describe the structure of an expectation. Perhaps it is the case that physical descriptions are uniquely applicable to physical levels of analysis, while mentalistic language is valid at the psychological and cultural levels of research. Again we are faced with a question which seems unaswerable: Is there a single appropriate language that will adequately describe the environment, or are many language potentially valid?

Clearly there are problems in delineating appropriate levels of analysis of the environment and in designing a language which adequately describes its features. Having said all this, I will bracket the question for now, and proceed to the body of this discussion of the nature-nurture question, albeit with a somewhat unclear conception of exactly what is meant by the term "environment."

THE "DEVELOPMENT FROM" PERSPECTIVE

The dichotomy between the "development from" and "development to" perspectives is of course a relatively artificial one, based primarily on the differences between the methodology and emphases of scientists characterized by each label. The temptation, however, has been for each to explain (sometimes explain away) the other's perspective under the umbrella of his own work. Recognizing that "development connotes orderly, organized change toward a hypothetical ideal," developmental theories of both types often "contain profound presuppositions about a *telos* and the hypothetical mechanisms that make change orderly and coherent" (Kagan, 1978).

Early developmental biologists and ethologists (roughly representing the "from" and "to" perspectives) seem to have established genetics at the center of their theories, thus making possible an account of *both* the mechanism or process, and the *telos* or endstates of development concurrently. Through the argument that much of development is genetically predetermined, both the developmental process and the purposive nature of development perceived by scientists (i.e., tadpoles turn into frogs, children learn how to count) can be taken care of under a single rubric. However, the tide of developmental science has more recently turned away from the notion that the genes autonomously determine both process and outcome. The environment has been awarded at least a facilitative role in development. Weiss (1970) takes a step further and argues that it is a

> widespread illusion that the course of development in general is lockstepped, microprogrammed in precisely

> branching chains of reactions, precisely arranged in space, and precisely timed as to rates and sequential order. The faith of those who hold such a micro-mechanical concept is in direct proportion to their degree of remoteness from practical experience with developmental phenomena.

Without the notion of genetic predetermination of both the developmental process and outcome, how can a developmental theory account for both? In this paper, I am presenting a dual approach to such a theory. This section centers on the "development from" perspective, and attempts to deal with the crucial question, If it's not in the genome, then where is the information for development? The implications of the answer--that the information can be found only in the relationship between gene and environment--are subsequently discussed as they impact conceptions of the nature of the developmental process; the inadequacies of an interactionist theory in considering "development to" an endstate then lead to the fourth section of this paper.

Where is the information for development?

I am presenting here a relatively abstract question -- just what does it mean? There are two different senses that one might be getting at. First, there is the question of what is ultimately possible in development: What information limits these possibilities? In other words, if I assert that it is impossible for a human to survive on a diet of hay or for a monkey to sing a Bach motet under any possible circumstances, what evidence need I have to support these assertions? On the other hand, one can speak of a second sense of

the question about the location of the information for development: Which factors determine what actually does happen in development? How does each contribute to the process? This approach is more suitable for the case of the male white-crowned sparrow: he obviously can sing (i.e., he has the capacity to develop song), but will he? What experiences and maturational events are prerequisite? It is this latter perspective on development which turns out to have the greatest value in answering the question, Where is the information for development?

The first form of the question is similar to that adopted by Scheffler (1980). However, while Scheffler has shown that it has great value in clarifying (and combatting) assumptions about what is possible in development, this approach may not be useful in understanding the developmental process. For example, if one is going to assert that X cannot do y, one must be ready to justify his assumptions about X and y. Some justifications can be easily based on genetic factors: Sally cannot digest cellulose because her DNA lacks the information for an enzyme that breaks cellulose down into a usable form. Furthermore, not only will Sally fail to digest cellulose, but so will Bill and Susan and every other member of the human species. Clearly there are some simple genetic factors that will, in any imaginable environment, strictly limit developmental possibilities.

Making such judgments about complex genetic or environmental factors may not be so straightforward. Individuals (like flies, for example) can have the same *genotype*, but develop different *phenotypes* in

in different environments (e.g., red eyes in a warm environment, but pink eyes when raised in the cold). In many, perhaps most cases, it cannot be ascertained that a certain genotype *cannot* result in y unless the environment has been defined and the situation verified as a result of experiment or experience -- and certainly there are infinite numbers of "possible worlds" to test. In other words, the assertion that "X cannot do y" may be true of a specific case in which both genetic and environmental assumptions are defined and are true; however, the general case of "if one is an X, then one cannot do y" may be a difficult assertion to prove, especially in the cases of complexly determined y's. There may exist possible worlds in which an X can do y. Although any X is of course ultimately limited by its genetic character, finding out what the limits actually *are* is difficult: the organism uses its genetic information differently in different environments. Thus, we can fairly confidently assert that "if one is a human, one cannot digest cellulose" because we can conceive of no possible world in which the cellulose-degrading enzyme will be produced by the human gut. However, an assertion like "if one has Down's syndrome, one will never achieve an IQ of above 120" could conceivably prove false in a world in which medical science effectively prevents or treats mental retardation, and educational methods successfully foster excellent performance on intelligence tests. These examples demonstrate the difficulty of demonstrating the ultimate limits of development, and suggest that this may not be the most fruitful approach to the question, "Where is the information for development?"

The other approach is to ask not "can it?" but "will it?" What *does* happen in development is determined by both the gene and the environment: knowledge of the genes or the environment alone is not sufficient to predict what physiological and biochemical processes will be active in the organism at any given time. This suggests that both the gene and the environment contribute information about development. It is easy to understand the concept of "genetic information" (whereas a hundred years ago this would have been futile) -- the sequence of bases in the DNA forms an alphabet-like code which is "read off" in the production of specific proteins, each of which performs a certain function in the body. The concept of "environmental information," however, is more difficult to conceptualize at this molecular level (although it poses no such problem at the level of the culture, for instance). In what manner can the environment supply information, even at the level of cellular biochemistry?

First, the environment provides some very real information in the production of a functional protein. Monod (1972) pointed out that "the (genetic) code is meaningless unless translated," and the process of translating DNA into proteins requires an environment as an energy source, as a supplier of amino acids (the "building blocks" of proteins), and so on. However, even more strongly, the cellular environment determines whether the string of amino acids that results from the translation and transcription of the DNA will fold up correctly and become a functional protein. Proteins (such as hemoglobin) are three-dimensional structures whose functional

properties hinge on their assuming a particular shape. Certain aspects of the cellular environment (like ionic concentrations) determine which of the literally thousands of possible three-dimensional configurations the protein will actually assume, and only one of these configurations is the functional one. Thus, at this most basic level, the environment provides information that is in no sense reducible to the genetic code.

Another manner in which the environment can convey information about development is through the "turning on and off" of genes. Although next to nothing is currently known about how genes are regulated during development, regulation occurs in day-to-day functioning and this model may be used as one possible mechanism of development. (The term "regulation" refers to those processes through which genetic activity is adjusted to fit the body's needs.) In *E. coli*, a bacterium on which much basic genetic research is performed, there is a system of genes called the "lac operon" that best exemplifies how genetic activity can be affected by environmental changes. In a situation in which the bacteria are grown in a medium containing nutrients like glucose but not the sugar lactose, glucose-utilizing enzymes (but *no* lactose-utilizing enzymes are produced. It is not the case that the bacteria are incapable of manufacturing the lactose enzymes: it turns out that the bacteria have a gene that codes for a *repressor protein*. This repressor protein is constantly produced, and in the absence of lactose in the cell medium, this repressor binds to a segment of the *E. coli* DNA and blocks the production of the lactose-degrading enzymes. Figure 1 should help in visualizing this case. Once lactose is introduced to

Figure 1. No lactose in cell medium.

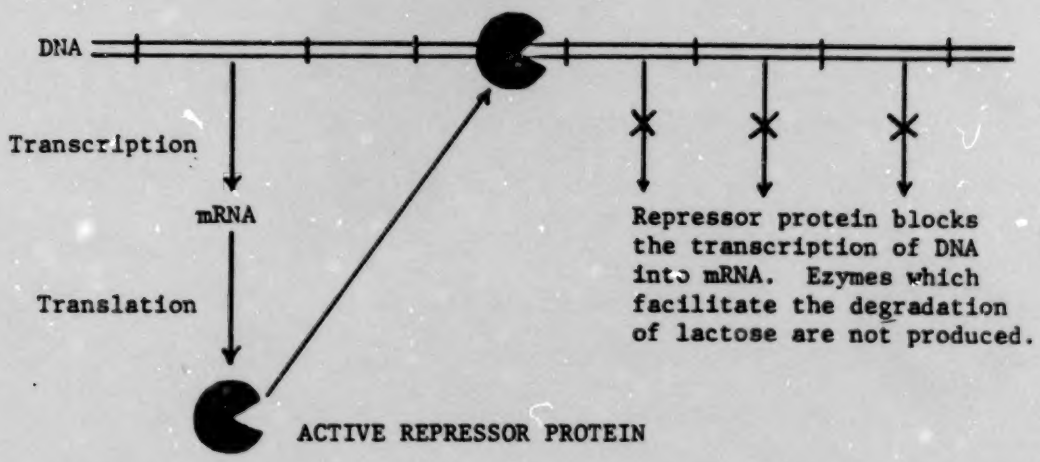
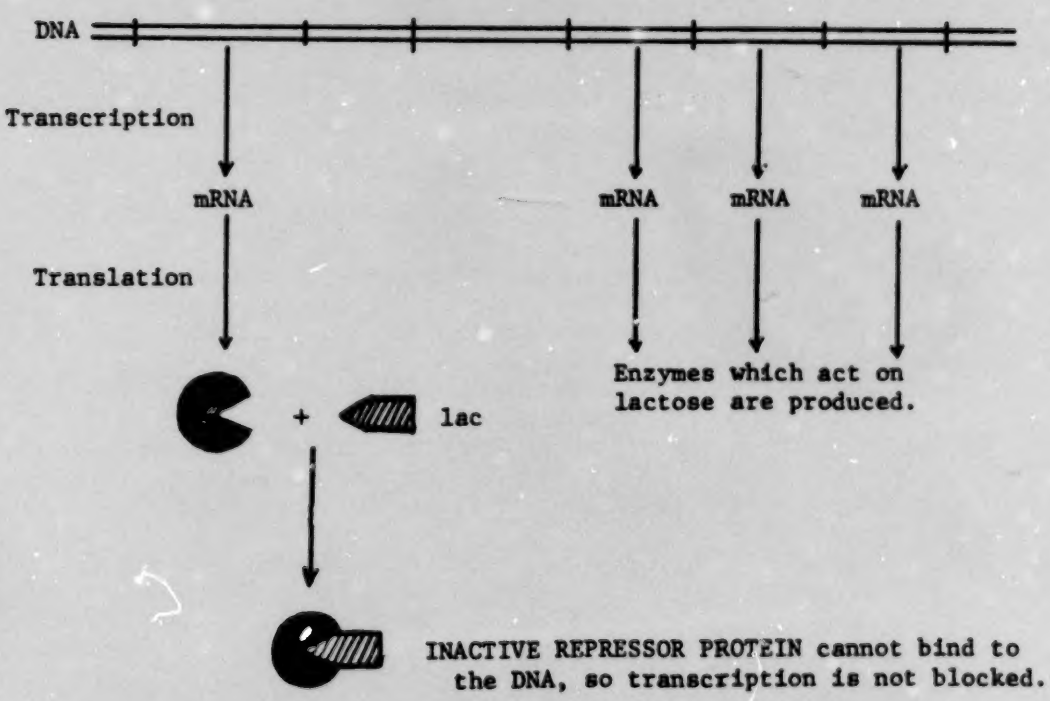

DNA
Transcription
mRNA
Translation
Repressor protein blocks the transcription of DNA into mRNA. Ezymes which facilitate the degradation of lactose are not produced.
ACTIVE REPRESSOR PROTEIN

Figure 2. Lactose is introduced to cell medium.



the medium, it forms a complex with the repressor; this *inactivates* the repressor protein and permits the lactose enzymes to be manufactured (see Figure 2).

An example of an analogous role of the environment in development may possible be found in the example of birdsong. Experiments suggest that in the spring, when the young male white-crowned sparrow starts singing his song for the first time, the growth of the areas of the brain which are responsible for song production is stimulated by the male hormone, testosterone (Nottebohm, 1980). There is a large body of work which suggests that in many birds, testosterone secretion is stimulated by the lengthening of the photoperiod (daylight) that accompanies the arrival of spring. Somehow, the perception of longer days seem to "de-repress" the genes responsible for enzymes that stimulate testosterone production in the male bird. The testosterone then facilitates the production of song. While this sequence of events is admittedly oversimplified and somewhat speculative, it does serve as a model of how developmental changes might be regulated by environmental as well as genetic input.

Clearly one can predict the course of an organism's development only given knowledge of both its genetic character and the environment in which it develops. Birdsong will not develop in a dog, nor in a white-crowned sparrow who has never heard song. This suggests that the information for development can be found in neither the genome not the environment alone, but rather that *the information for development is in the relationship between the genome and the environment*. This position has often been termed "interactionist"; what it means is that development cannot be attributed to the genes alone, nor to the environment alone, nor even t[illegible] addition of genetic and

environmental factors. In other words, development is a result of an interaction of two components; the result is something qualitatively different than either component. Kagan (1978) uses a physics metaphor to describe how psychological phenomena result from an interaction between an element (a particular neural structure) and a larger field (the whole central nervous system), but the analogy seems equally valid in understanding the relationship between the genome and the environment in development:

> Physics provides the best metaphor: An accelerating electric charge is placed in an electromagnetic field and they mutually influence one another. The charge is described in terms of velocity and energy, the field in terms of strength, and their interaction produces a third, quite different phenomenon, radiation, which is described in terms of frequency. The radiation is neither part of the field nor part of the charge; it is a product of the interaction of charge and field.

Galambos and Hillyard (1970) summarize this interactionist perspective in developmental biology:

> Most developmental biologists accept that each characterizable stage of embryonic (or cellular) differentiation is the product of its immediate predecessor's lawful interaction with an appropriate environment; no stage springs *de novo* or exclusively from a pattern of genetic activity.

Understanding the interactionist perspective on development makes it obvious that one simply cannot, for convenience or for any other reason, separate the developmental process into two separate, additive components, one genetic and the other environmental. In no case can you have radiation without a charge or without a field influencing the outcome. This understanding has prompted numerous biologists, among others, to reject the nature-nurture debate entirely, exclaiming, "But there is no problem!" -- one must always speak of one when one speaks of the other in the context of development. (Part of this rejection stems from an interpretation of the words "nature" and "nurture" that differs from that held by many psychologists. I will

return to this point in a later section.) However, recognizing the validity of this conclusion-- that there is no real nature-nurture problem in the sense of which controls the other -- does not emancipate developmentalist from studying the roles of both in development, just as the physicist cannot study how radiation is produced while ignoring charge and field. The remainder of this section on the "development from" perspective will examine the problem of accommodating this interactionist perspective in a theory of the developmental process.

The environment: Constructive or permissive?

Obviously the environment plays a decisive role in development -- but what is the nature of that role in a developmental theory? Such a question moves us away from a scientific study of interactionism toward a more philosophical distinction between some possible roles. Much of "popular" genetics and biology (e.g., Monod, 1972; Wilson, 1979) is based on the notion that development consists of an unfolding of essences within the genome. Certainly the environment contributes to the process of unfolding, but in this view it contributes in a *permissive* manner, by allowing certain genetically based paths to take their course. An alternative view is that the environment, as well as the genome, contributes *constructively* to development. This implies that the outcomes of development cannot be attributed to the genome as a primary source, with the environment providing merely supplementary information. The distiction between the two views is largely philosophical since neither contradicts the scientific view

of interactionism, but I strongly favor the latter, constructivist perspective.

Consider the following examples of what I have termed the permissive view. Although each is obviously a shorthand for describing a complex and intricate process, they serve to pinpoint an assumption prevalent in many popular and scientific considerations of nature and nurture, that the genome specifies the array of potential capacities and outcomes, while the environment permits certain of these to be actualized:

> ...the genes create a unique substrate that allows a language repertoire to expand from zero to that of a loquacious adult, and the environment determines which of the thousands of known languages the child will actually speak. In this, as in most samples of behavior, the genetic readout specifies the capacity, while the environmental stimuli determine its specific expression and content. (Galambos, 1970)

> At each (developmental) stage more highly ordered structures and new functions appear which, resulting from spontaneous interactions between products of previous stages, reveal successively, like a blossoming firework, the latent potentialities of previous levels. The determining cause of the entire phenomenon, its source, is finally the genetic information represented by the sum of the polypeptide sequences, interpreted -- or, to be more exact, screened -- by the initial conditions. (Monod, 1972)

This notion of development as a "revelation" of the genetic code (Monod, 1972), with the environment acting in a manner which permits this revelation to take place, assumes that there are readily identifiable and appropriate *endstates* of development. The forces responsible for guiding the developmental process are considered primarily in light of the "development to" perspective, and the determining essence of some valued endstate is seen as somehow latent in the genetic readout.

The alternative to this point of view is that there is no essence, and that there are no particular endstates that are aimed for during development. (Obviously, adoption of this perspective would pose some problems in accounting for the "development to" perspective.) Rather, in this view outcomes are constructed in the interaction between gene and environment. Many particular outcomes can result from different gene-environment interactions; the functionality of a particular form in a particular environment is a result of chance occurrence caught through evolution in that environment, and not of a predetermined course of development which has the goal of releasing the genetic essence. This view suggests that the environment plays a constructive role in shaping normal, adaptive endstates just as it does in the development of aberrant outcomes. Indeed, in this view, development is seen as a perhaps uncomfortably chancy process, a complex and intricate system which defies the confident predetermination which one might like to ascribe to it. Weiss (1970) would like to "uproot, once and for all, the naively preformistic notion of neurogenesis as simply the blind, piece-by-piece conversion of a minutely mapped-out cell mosaic into the configuration of the final product." He describes the development of cells in the nervous system from this perspective:

> Their fates and paths are still indefinite in detail and gain their unique definitions through continuous interactions with unpredictably varying constellations of their local environments. The latter, in turn, are functions of an equally varied past epigenetic history of the whole system.

The question of whether the environment permits or constructs outcomes may not be resolvable scientifically. Each way of looking at the role of the environment recognizes its crucial role in devel-

opment; neither diammetrically opposes interactionism. Philosophically, though, the distinction is clearer. The notion of the environment as permissive is grounded, if not directly in Aristotelian essences, then minimally in the idea that development moves purposively toward some endstate. It has been pointed out be Scheffler (personal communication), however, that what we see development as moving toward is a matter of one's perception. Aristotle viewed the essence of the acorn as the oak tree, but even more commonly acorns become mulch, food for squirrels, or tiny saplings to be eaten by deer. It could, of course, be argued that these outcomes are ecological, not developmental phenomena -- if the acorn is to develop at all, it develops into an oak tree. Manipulating the environmental conditions during development, though, can result in changes in the process and in altered, even novel, outcomes. The proponent of the view that the environment is permissive may dismiss abnormalities as unimportant, or even misleading. Alternatively, he may cite the hypothesis that the genome specifies the range of potential outcomes: thus, the abnormal outcome is simply one possibility in this range, and the experimental manipulation permits it to develop.

I think that an evolutionary perspective on this facet of the problem lends greater credence to the constructivist viewpoint. Marshack (personal communication with H. Gardner) commented that if humans today were to face a radically different set of environmental circumstances, potentials unimagined now would be realized in practice and, in all probability, in the physical function of the brain, even though our genetic constitutions would remain at first largely unchanged. Certain it is problemmatic to claim that these new potential-

ities are lying latent in the genome, waiting for an environment unencountered in our evolutionary history to permit their actualization. Similarly, when a kitten is raised from a very early age wearing special goggles that allow the kitten to see lines only of a certain orientation (for example, only verticals). When the kitten grows to adulthood, the neurons of its visual cortex respond only to vertically oriented lines. This development is presumably a first in the cat's evolutionary history; yet how can this particular outcome be one of a range of potential outcomes specified by the genome if the genome has never encountered and surely cannot have "known" about this environment? Between this seemingly unresolvable dilemma and the essentialism that seems inherent in the permissive view of the environment, I am inclined to reject this view in favor of labelling the role of the environment in development as constructive. However, a pair of epigenetic developmental theories further elaborate the differences between these two alternative views.

Probabilistic epigenesis

This discussion of the "development from" perspective forces a realization that any answers to questions about the nature of the developmental process must involve a consideration of a host of complex factors in the interactions between the genome and the environment. This view is a radical shift away from a traditional biologically-based theory of development, but it leans closer to another, more modern theory. By and large, all theories of biological development are based upon the concept of *epigenesis*. Monod (1972) explains its origins:

> The appearance of new structure and new properties in the course of embryonic development has often been referred to as an "epigenetic" process, expressive of the gradual enrichment of the organism as it grows from its bare genetic beginnings represented by the initial egg. The adjective is also often employed in reference to now outmoded theories in which the "preformationists" (who believed that the egg contained a miniature of the adult animal) were lined up in opposition to the "epigeneticists" (who believed in an *actual* enrichment of the initial genetic information).

Epigenetic theory is presently much more than a simple denial of preformationism, though, and has been adopted in many psychological as well as biological theories of development. Kitchener (1978) lists five tenets common to epigenetic theories of development:

> Epigenesis, as described by most developmental biologists, has five essential features: it is a causal sequence of events, it is a series of stages or levels, it is a process of differentiation, it involves an increase in complexity and organization, and it involves emergent properties.[3]

The interactionist view of development encounters different fates with different versions of epigenetic theory. There are two major versions in biology: predetermined epigenesis and probabilistic epigenesis. The latter better represents the interactionist perspective. I will discuss each of these versions in terms of their explanations of behavioral devleopment; however, the concepts described may be seen as equally valid in dealing with the development of other systems.

Early epigeneticists came up with the theory of *predetermined epigenesis* as an epigenetic offshoot of preformationism, in the sense that each concept is based on some form of hereditary determination. Gottlieb (1970) outlines the characteristics of the two versions of

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[3] The reader is invited to consult Kitchener (1978) for further discussion and a criticism of these features.

predetermined epigenesis:

> Both views have the assumption that the behavioral sequence is predetermined by factors of neural growth and differentiation (maturation), which have an essentially invariant schedule of appearance. In this view, *nonsensory environmental factors merely support developmental or allow behavioral development to occur and sensory stimulation does not influence or determine the course of behavioral development in any significant way.* (Emphasis mine.)

Through this kind of theory, the biologist can explain the developmental process in embryological/maturational terms, and can account for development toward evolutionarily adaptive endstates -- functional behavior -- in the assertion that they are predetermined in the maturation of the nervous system. Predetermined epigenetic theory clearly runs counter to the premise and findings of this paper: I have argued that, from both a scientific and a philosophical perspective, the environment as well as the genome must be allowed an active, constructive role in development. It is clear from experimental evidence that sensory stimulation can and does "influence or determine the course of behavioral development." Recall the kitten raised wearing the special goggles which allowed it to view only vertical lines. Also, another experiment performed on kittens has demonstrated that it takes the experience of coordinated visual input (two eyes focussing on the same object at once) for binocular vision to develop in the cat (LeVay et al., 1980). In other words, neural maturation itself can depend on sensory stimulation. As far as nonsensory environmental events merely supporting or allowing development, this is a case of the environment viewed as permissive, an argument which I have concluded is philosophically unsound.

There is, however, another version of epigenesis which is more

sympathetic with an interactionist perspective. This version was generated by research in behavioral embryology which ran counter to the notions of predetermined epigenesis, and is called *probabilistic epigenesis*. According to Gottlieb (1970), there are three ways in which probabilistic epigenesis differs from predetermined epigenesis. First, the action of "stimulative factors" -- sensory stimulation, function in certain systems, etc. -- in development necessitates some degree of uncertainty in behavioral development. Weak events may simply facilitate the development of behavior along certain lines, while stronger events may channel or force development into certain paths. Thus, the developmental course cannot be predetermined since the course depends on or is selected as a result of environmental stimulation interacting with genetic factors. Since environmental information is largely probable, rather than given as is the genetic information, development along a certain path must be viewed as probabilistic, not predetermined.

Second, while predetermined epigeneticists view the relationship between structure and function as unidirectional (structural maturation determines function nonreciprocally), probabilistic epigenesis posits a bidirectional structure-function relationship: function can significantly modify the development of the structures involved in that functional event. For example, embryonic chicks still in the egg show random movements which are independent of sensory stimulation or feedback in the early stages of devleopment. If, however, the chick embryo is paralyzed for as little as one to two days during development, a variety of malformations in the joints of the legs, toes and neck

results (Gottlieb, 1976). This exemplifies a bidirectional structure-function relationship in that motor movements are a consequence of function in the skeleto-muscular structure, but the movement itself influences the development of the underlying structure, presumably by affecting the genetic activity of the cells which constitute the structure. Thus, while the older, predeterminist view can be summarized by the relationship:

Genes ⟶ *Structural Maturation* ⟶ *Function*,

the probabilistic view posits the relationship in a bidirectional manner:

Genes ⟷ *Structural Maturation* ⟷ *Function*

(Gottlieb, 1976). Gottlieb goes on to argue that this representation does not undermine the importance of other factors in development:

> In the past, it has not been usual to consider neural activity, sensory stimulation, feedback from motor movement, etc. as normal features of neuroembryological development. The incorporation of function as a factor in the late stages of neuroembryological development does not disregard or underrate the powerful nonfunctional contributions to neural maturation (e.g., sprouting, neurotrophic factors); it only widens the traditional purview. (Gottlieb, 1976)

Thus, genetic, sensory environmental and nonsensory environmental factors are each granted a powerful and constructive contribution to the process of development.

Gottlieb (1970) makes a third and final contrast between the two theories. He maintains that predetermined epigenesis emphasizes discontinuity in development arising from spurts in the maturation of

the nervous system. In contrast, the probabilistic viewpoint centers on the "gradual and continuous development of behavior in line with the hypothesis that stimulation or motor patterning of some sort is almost always involved in one way or another in the activity of the embryo or fetus." Gottlieb emphasizes the view that behaviors which are often called innate (like the "automatic" pecking behavior of a newborn chick) can be traced to, and are dependent on, behaviors which occurred in earlier states. Surely this latter point is well taken: maturation is dependent on experiential and other environmental factors,[4] so behaviors may not be emergent in the sense that they arise solely out of and due to genetically-guided maturation. Yet while it is clear that there is continuity in the developmental process, as Gottlieb maintains, I would argue that there may well be points in development when the rapid maturation of neural systems -- which occurs as a result of both genetic and environmental events -- suddenly opens up the potential for the emergence of new behaviors which are quite distinct from the functions which led to their development. Although this may lend an appearance of discontinuity in development, it need not imply discontinuity in process. In other words, behaviors like babbling in a young child might indeed appear emergent in the sense

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[4] Many terms are being bandied about in this section: gene, environment, structure, function, experience, to name a few. I am presently permitting myself to implicitly allow "experience" and "function" to be subcategories of "environment," in the sense that none of these could be rightly called "genetic" or even gene products. There is, however, a potentially valid case for claiming that some functions or experiences are more rightly placed under the banner of "nature" rather than "nurture" if the functions are autogenous. I will examine this problem in greater depth in a later section of this paper.

that they are new behaviors, and they are certainly grounded in neural maturation, but the maturational process itself results from a host of genetic and environmental or functional factors interacting in a manner much more complex than a reading off of the genetic code.

Probabilistic epigenesis thus differs radically from predetermined epigenesis in its assertion that experience, via a bidirectional structure-function relationship, may guide or facilitate development, as opposed to the notion that the behavioral sequence is predetermined in an invariant schedule of neural growth and maturation. Gottlieb (1970) summarizes this stance by holding that "the behavior of individuals within a given species does not follow an invariant or inevitable course, and, more specifically, that the sequence or outcome of individual behavioral development is probable (with respect to norms) rather than certain." This theory of development is quite amenable with the notion supported in this paper that the process is solidly and inextricably grounded in the interaction of genetic and environmental factors. Probabilistic epigenesis entails no implicit or explicit notions of essentialism or the predetermination of outcomes. Thus, for these reasons, probabilistic epigenesis is a braod-based theory tenable to biologists -- and even psychologists -- with an interest in exploring both the genetic and environmental factors that contribute to development. It is, however, a process-oriented or "development from" theory in that it concentrates on how development proceeds; the following section will examine the impact of adopting such a theory on the "development to" perspective.

THE "DEVELOPMENT TO" PERSPECTIVE

We have been considering development from the "development from" angle, asking such questions as: What information is responsible for guiding development at any given time? What sorts of processes might serve as the mechanisms of gene-environment interaction? To what different endstates can altering the genetic or environmental factors lead? The answers to these questions are quite complex, and they lead to a view of the developmental process as an intricate network of incessant interactions between the genetic material and its cytoplasmic, cellular, and extraorganismic environments. The problem that now seems most puzzling is not how it is that development can lead to a variety of particular outcomes, but rather how it is that there can be such similarity in development in the face of unpredictable, random fluctuations in the environment.

In this vein, Lerner (1978) has pointed out that "an infinite array of potential phenotypes could be produced from an interaction of...one genotype with the infinite array of experiences it could encounter." (It is this observation that probabilistic but not predetermined epigenesis can account for.) Lerner goes on, though, to write, "However, although a biological reality, the norm of reaction of any genotype is immediately delineated at conception since a genotype must be expressed in one particular environment...." In other words, while the developmentalist may manipulate environments to his heart's content, creating new endstates in the process, the scientist of the "development to" perspective is more interested in the fact

that wrens eventually sing and children learn to count and talk. He is primarily concerned with how development proceeds to these endstates which are likley to be expressed given the organism in a normative environment. Thus, armed with retrospective information about the developmental outcomes of certain species in certain environments, he may identify species-typical behaviors or phenotypes as endstates common to the species. A theory of development must deal with development to these endstates as well as with development from any state, but it must do so, in accordance with the lessons learned in the study of "development from," without attributing to the genome the essence of the outcome. An especially difficult task is to account for the "self-righting tendency of the organism" to develop along a path, or what seem to be *central tendencies* of the genome to develop to certain endstates, even in the presence of apparent deterrents to this development.

It is heuristic to explain these central tendencies in development through a convenient shorthand, assuming the details of the process or *how* the interactions occur. In biology, the usual way of viewing development to an endstate along a proscibed developmental path has been expressed with the metaphor of the genome as a blueprint for development. When taken literally, however, this metaphor has misrepresented the "development from" perspective. In this section, I will examine the "genome as blueprint" shorthand, point out both its uses and some flaws, and then offer the notion of conditional probabilities in development as an alternative shorthand, building on Gottlieb's

(1970) notion that "the sequence or outcome of individual behavioral development is probable (with respect to norms) rather than certain."

The genome as a blueprint for development

Many developmental biologists spend their entire careers trying to understand the mechanisms of development within one particular system of one or two species -- clearly, no shorthand can possibly do justice to the myriad complex and intricate interactions that characterize development in each of these systems. Thus, at best, the metaphor of the genome as a blueprint for development is a useful heuristic which enables one to view the entire course of development with getting bogged down in its overwhelming complexity. However, at worst (and more commonly), the metaphor is interpreted literally to misrepresent the developmental process as static and predetermined.

Although interactionism in development has been well-established scientifically, there are many instances in which this interactionism is taken for granted, in cases in which the environmental events that are essential for constructing an endstate can be counted on. For example, the physical maturation of the embryo is often referred to as under the control of the genetic blueprint; although certainly the embryonic environment is crucial in this process, it is also true that that environment is highly regulated and, in most cases, one can assume that what should happen indeed will. Scheffler (1980) has pointed out that when the presence of interactive factors can be counted on, development seems to approximate a "continuous series"

model, in which development proceeds like a row of dominoes falling down, A hitting B causing C to fall and so on until finally Z is knocked over. Thus an ethologist who studies the pecking behavior of newborn chicks may attribute the precise timing of emergence of this behavior to the genetic blueprint *in spite* of his understanding of interactionism and *in spite* of his knowledge of the environmental events and embryological experiences necessary for the development of this behavior. He uses the genetic shorthand because he can essentially count on the occurrence of these factors and experiences; the environmental interactions are expected to occur. Thus, out of convenience, development may approximate a genetic continuous series.

This shorthand can have disastrous consequences, both scientific and political, if not properly qualified. Kitchener (1978) points out that among developmental biologists who use this shorthand, there may be no such implicit interactionism; there is rather "the view that there is a predetermined (inborn, genetic) program -- a set of instructions or algorithms -- setting out the course of development...." This, of course, rings of the predetermined rather than probabilistic view of development, one which I have tried to demonstrate is unsound. Thus it is not at all unlikely that use of this shorthand will be interpreted as support of predeterminism, regardless of the views of the user. The political overtones of developmental analysis based primarily on genetic considerations have also become heightened in recent years, especially in the controversies surrounding sociobiology.[5] Clearly, it is not to be taken for granted that

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[5] As long as a behavior has *some* genetic basis, one need not insist

use of the "genetic blueprint" shorthand will be taken as a heuristic even if one plants oneself solidly in the interactionist camp of the nature-nurture debate. The phrase means different things to different people; perhaps it is time to devise a fresher shorthand, one intrinsically more sympathetic to the interactionist perspective, for, at the very least,

> A facile description of the genome as a "blueprint" gives a misleading impression of understanding a problem that is regarded by modern geneticists as one of the major unsolved problems of biology.... (Lehrman, 1970)

The central tendencies of the genome examined

Central tendencies, buffering mechanisms, homeostasis -- all of these are ways to describe what seems to be a "self-righting tendency" of the organism to keep itself on its track of development. To what extent is this tendency to be considered part of the genome? How can one explain these tendencies without contradicting what has been learned from the "development from" perspective? This is a subject about which "development to" has a lot to say.

The organism does indeed appear to be genetically prepared for certain environmental events -- both events one would expect to direct the organism onto the right track of development, but also those which would seem to deflect the organism from the normal path. Take, for example, the strong tendency of the male long-billed wren to

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that the development of the behavior itself is "genetic" in order to support sociobiology, nor does a refutation of this view discredit sociobiological theories of the evolution and adaptiveness of behavior.

learn its conspecific song. Male wrens born in early summer are exposed to the songs of adult males throughout June and July; learning of song is restricted to the first sixty to eighty days of life. By this time the birds have developed a relatively sophisticated song repertoire and are thereafter unable to learn new songs. These first eighty days of life have thus been termed the critical period for song learning in long-billed wrens. Kroodsma (1978) discovered a paradox in this system, though: the last crop of nestlings hatch *after* the adult males have stopped singing for the year -- thus, wrens born in late summer hear no adult song during their critical period of song learning. Apparently what actually happens is that in these late-born males, the critical period for song learning is extended to the following spring.[6] Although these males do develop subsong[7] in the fall (but only to a very rudimentary level), it is not until the following spring that these birds learn to sing (Kroodsma and Pickert, 1980). It is thought that the delay of the critical period is due to the joint effects of not hearing any song early on and the suppression of testosterone, which stimulates neural development in the song production areas of the brain, due to the shortened photoperiod in the fall. Thus, it is apparent that there are at least two alternative developmental sequences leading up to song production in the male long-billed wren, one employed by the majority of wrens born in early

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[6] In experimental situations, August-born males that *do* hear the song of adult males during the first eighty days do develop appreciable song repertoires during this time (Kroodsma and Pickert, 1980).

[7] Subsong is a noncommunicatory vocalization made by the young male. It is somewhat reminiscent of the cooing and babbling stages of vocal development in infants (Nottebohm, 1980).

summer and the other employed by the fraction of late-born nestlings.

This example demonstrates that not only is a strict "genetic timetable" model of development inappropriate to describe a system that clearly depends upon an interaction between genetic and environmental factors, but it also becomes apparent that, in some broad sense, the genome *expects* certain environmental events to occur in development. As was mentioned in a footnote, a behavioral system must have a genetic basis in order for natural selection to act on it; however, nature selects for the outcomes of the interaction between that genome and its normative environment, not for the genome itself:

> Nature selects for *outcomes*. Natural selection acts to select genomes that, in a normal environment, will guide development into organisms with the relevant adaptive characteristics. But the path of development from the zygote stage to the phenotypic adult is devious, and includes many developmental processes, including, in some cases, various aspects of experience. (Lehrman, 1970)

"Development to" thus runs along a general path, expectant of certain -- perhaps any of several -- environmental events to occur. Development to an adaptive endstate is *environment-expectant*. Galambos and Hillyard (1970) put this expectancy in the light of the details of the process itself:

> In terms of molecular biology, a specific gene-enzyme-structure pattern is active at each (epigenetic) stage, making the embryo receptive to a restricted range of environmental substrates. Any such substrates present are incorporated into their waiting molecular niches, changing the morphological structure and initiating a new pattern of gene-enzyme activity, thereby creating the next stage with new substrate preferences. And so forth. The course of development is thus governed by the sequential throwing of genetic switches, the exact pattern of switching being a cofunction of the extant structure and the external impingement.

Thus the genes of the long-billed wren have been selected for, at least in part, because in either expected environment -- early or late hatching -- song still develops in the male.[8] The central tendency of song learning itself can be thought of as a *set of processes* based upon expected gene-environment interactions and selected through the course of evolution rather than as a property of the genome. Weiss (1970) has noted that evolution can fashion, for example, extremely complex control networks for regulating normal blood pH or for modulating limb movement and posture in proprioceptive circuits. There as no reason that evolution could not fashion similarly complex buffering processes in development -- processes which modulate a range of environmental fluctuations and channel the organism into a certain outcome. However, Weiss (1970) notes that these processes can only be fashioned out of "*past* evolutionary experience with major contingencies of rather consistent recurrence." As the probabilistic epigeneticists have shown, there are environmental events that can throw development to an endstate off track; however, it seems that evolution has fashioned a genome that can react advantageously to a range of recurring environmental conditions. It need not plan for any random environment.[9] Thus, rather than positing

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[8] Kroodsma et al. (1980) offer evidence that the early and late hatching schemes are advantageous to the long-billed wren as the different sensitive periods facilitate dispersal strategies and territoriality in the species. The reader is referred to this report for further elaboration.

[9] There are reported instances in which the environmental events expected in development do not in fact occur, yet development still

the central tendencies in the genome itself, in an essentialistic fashion, the "development to" perspective suggests that these tendencies are a set of developmental processes, evolved under certain recurrent conditions, which tend to buffer the organism as it develops in the environmental range under which the tendencies evolved. Thus, through natural selection, the long-billed wren has evolved what we call a central tendency toward song production, but the tendency itself is based on at least two alternative processes of interaction between a genome and evolutionarily recurring environments; each interactional process results in the same adaptive endstate -- song. Weiss (1970) summarizes:

> One might submit that evolutionary experience has endowed the germ with tolerances, that is, allowances for the variety of unforseeable, hence unpredictable, contingencies each specimen is bound to meet in its real and unique course of development....(However,) evolution can fashion ...mechanisms that have proved effective in meeting circumstances of constant repetitiveness....
>
> In short, structured neuronal feedback loops, such as those of the carotid and proprioceptive reflexes, molded by *past* evolutionary experience with major contingencies of rather consistent recurrence, cannot be put forward as rationale for claiming universal evolutionary prescience, as it were, of the myriad of minor and fortuitous *future*

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appears to be channeled along to some endstate. For example, when a child is born deaf or a sparrow fails to hear conspecific song during the critical period, each still shows a strong tendency to develop its species-typical form of communication. The deaf child may spontaneously develop a form of sign language replete with a grammar of subject, action, and object (personal communication with H. Gardner), while the sparrow will improvise a highly abnormal song (Nottebohm, 1970). My guess is that these cases are not so much examples of the emerging essence of the genome as they are instances showing the tendency of the neural substrata of these behavioral systems, developed already at least to some extent prior to the expected environmental experience, beginning to function in the manner for which each has been set up.

> fluctuations of conditions during each individual and unique ontogeny. System dynamics provides for this primary general adaptiveness.

So, not only do we have a view of development which rejects genetic predetermination of outcomes, we also have a view that recognizes many alternative routes to the same adaptive endstate; these routes fall under the umbrella term of a "central tendency." Thus, the metaphor of a genetic blueprint for development has become less and less appealing with improved scientific understanding of the process -- that the blueprint itself is dynamically unfolding with environmental input -- and with a clearer view of how development to an endstate proceeds -- by any of several routes, the particular one followed being constructed out of a particular interaction between gene and environment. It's time to look around for a new shorthand, I think.

Conditional probabilities

It is no small challenge to devise a shorthand which treats development as both environment-dependent (the environment has a constructive role) and environment-expectant (development to an endstate expects certain environmental events to occur),[10] yet gives full due to the role of the genome in the process. I will begin this attempt by examining development to species-typical endstates, outcomes in which the genetic character is thought to have a strong "directive" role. The result of this consideration is the intro-

[10] These terms and conclusions have also been expressed by Bekoff and Fox (1972).

duction and elaboration of the concept of *conditional probabilities* in development. I have chosen to adopt a language which describes development to an endstate in probabilistic terms of the environmental conditions that must be met, often at specified times in development, and may be differentiated according to the type of role that each has in development. These conditional probabilities take the general form: *If parameters A and B of the environment are present (at points in time* t_A *and* t_B*) during the development of an organism of a certain species* O_s*, then there is a probability p that species-typical end-state* E_s *will be achieved.*

The probability that development will proceed to E_s depends on two factors: the completeness of the information about the conditions required for development, and the extent to which the developmental process incorporates purely random elements. In other words, weaker probability statements must be made in the case of statements that describe fewer of the necessary conditions that must be met. For example, the statement "if a long-billed wren hears adult conspecific song during the first sixty to eight days of its life, there is a probability p that the wren will develop song itself" will necessarily have a small p. Several other necessary environmental parameters can be crucial to song learning. If the wren is a female, song will develop only if testosterone is applied exogenously. Even if the wren is a male, oxygen deprivation or an extremely high temperature could also block song learning (to say nothing of life itself). Linsky (quoted in Fodor, 1980b, p. 99) has said, "Never try to give necessary and sufficient conditions for anything"; this advice is well-taken. It

is largely unreasonable to expect to come up with 100% probability statements, for two reasons: first, because a proposed list of necessary and sufficient conditions can be enormously long yet not be truly sufficient -- there may be factors present of which we are unaware -- and second, because a 100% probability statement is logically impossible due to the inherent random nature of some developmental processes. Genetic replication, transcription, and translation contain small but very real probabilities that random mistakes will occur. At another level, randomness plays a role in cellular differentiation and growth: identical twins have the same overall distributions of pigment, but their freckles are not in the exact same places; nor do their brains show the same microanatomical structures (Weiss, 1970). While random elements need not, and indeed seldom do, necessarily deter "development to" from its path, the small possibility nevertheless exists.

We now have a framework on which to build. "Development to" can be described in terms of an organism (assuming a "species-typical" genome"), a set of environmental conditions that are necessary, but never sufficient, for the development to the endstate, and an estimate of the probability that the endstate will indeed be achieved given that all these factors are met. These statements are testable experimentally, open to both genetic and environmental limitations, and relatively independent of explanations of how the developmental process itself works. The next task will be to delineate different ways of classifying the environmental factors in order to further simplify this approach in order that it may be useful even though it does not propose to specify all the necessary and sufficient conditions needed.

Four categories of environmental factors

Since one cannot list the necessary and sufficient conditions for development, yet "development to" must be described in terms of necessary environmental conditions, it would be useful to develop a language in which one can group various categories of environment and experience, both for the sake of convenience and for the sake of better understanding the different types of effects that the environment can have on development. I will attempt this by first describing an example of a system in which different types of interaction take place in development, then building around it a vocabulary for addressing these different types of factors. Four conceptual categories of environmental conditions result: essential conditions, emergent conditions, necessary conditions, and requisite conditions. Use of these categories should simplify lists of the conditions required for "development to," especially when there may be conditions that have not yet been experimentally verified.

Again in light of the view that nature selects for outcomes, not processes, it becomes clear that species-specific features may develop through genetic action with minimal environmental input, or through maturation based on the interaction of many conditions or experiences that may be expected to occur in the species environment. I will use the case of the development of neurons in the visual cortex to outline some different types of environmental interactions. The visual cortical neurons of both kittens and humans develop certain physiological selectivities early in life -- for example, some neurons respond only

to lines of a horizontal orientation, while others respond only to verticals; some receive input only from one eye, while others receive input from both. Some of these selectivities seem to develop fully within the uterine environment, and require no direct visual experience. Others, like the sensitivity to lines of particular orientations, are detectable in the newborn but are "fine-tuned" through experience with an environment composed of verticals, horizontals, and contours. Raising a kitten in a visual environment composed only of verticals will result in a visual cortex responding only to vertical stimuli. Finally, binocular vision (in which neurons respond to stimulation from both eyes) develops only with the experience of coordinated input from both eyes. If this coordinated input is prevented for some reason -- either a bad astigmatism in one eye which badly blurs vision, or a strbismus in which the eye muscles are misaligned and the two eyes cannot focus concurrently on an object -- then binocularity fails to develop in the visual cortex. In fact, about 6% of sample human populations are affected by a condition called amblyopia, a long-lasting impairment of binocular vision resulting from disturbances of coordinated vision in early life. It has been speculated that this condition might actually benefit the person affected by it (in times before ophthalmology), since in this condition the good eye tends to suppress the bad eye, maximizing visual acuity. The development of binocularity is potentially more disruptible than that of orientation specificity in species-typical development, although each depends on visual experience for its development. Note that it is a property of every known

human environment to be composed of contours extending in all directions, yet it is not a property of every human to be able to focus both eyes concurrently on an object.

The above example suggests that there may be qualitatively different kinds or categories of environmental influences on development. As an initial attempt at discriminating among the possibilities, I here present and define four categories of environmental conditions for the achievement of E_s. (In accordance with the conclusions reached in the section on conceptions of gene and environment, many levels of environmental influence, from cytoplasmic to cultural, are included.) Briefly, they are:

1. *Essential conditions.* These are environmental conditions, independent of functional experience, without which the organism, by its very nature, cannot exist. For example, the biochemical pathways of all animals are based upon an expectancy of a suitable range of concentrations of oxygen and water, and the presence of nutrients. Especially in the case of very simple organisms, some structures may develop in the presence of only these essential conditions, independently of the functioning of the structure (although quite frankly I find it improbable that any system could develop completely independently of any functional feedback).

2. *Emergent conditions.* These are functional experiences which arise from structural development, and feed back to further affect development in the original or in other systems. These functional experiences are independent of external sensory input or feedback. The autogenous movement of the embryological chick, without which its joints

become malformed, can be considered an example of an emergent condition. These conditions may be especially difficult to demonstrate experimentally, and may be considered jointly with essential conditions as they seem to emerge out of those essential conditions.

3. *Necessary conditions.* These conditions, while they are urgent for the achievement of E_s, are not essential to the organism's survival, nor do they arise autogenously. However, although sensory or non-sensory input is crucial to the achievement of E_s, E_s is not dependent on the specific "content" of the input. For example, the development of binocular vision is dependent upon the experience of coordinated visual input; binocular vision develops, however, regardless of the particular content of the environment focussed upon by the two eyes. A rock is as good as a face is as good as a pair of vertical lines.

4. *Requisite conditions.* Like necessary conditions, these are neither essential to the organism's survival nor are they autogenous. Unlike necessary conditions, however, requisite conditions follow from other circumstances and are imposed externally rather than by the nature of the subject. The specific content of the environment directly affects the manner of expression of E_s. For example, it is the nature of the environment to be composed of contours in all orientations; thus, the development of all orientation sensitivities is stimulated in visual neurons of normal cats. However, imposing an environment of verticals alone on a young kitten tunes up the neurons initially responsive to vertical stimuli, and also causes neurons with other initial sensitivities to become sensitive to verticals instead (and those which are not transformed become unresponsive to any input).

The following section will test the use of these categories in the study of development to an endstate, employing the now-familiar example of the development of birdsong. It is hoped that these categories will make explicit recognition of the possible roles of the environment and experience in development to an endstate, particularly when such roles might be glossed over or assumed by a genetically-oriented shorthand. They should also facilitate recognition of environmental contributions to development, even when the exact nature of these contributions (in terms of the developmental process itself) has not been explicitly worked out.

Conditional probabilities in the development of birdsong

Among birds there exists a tremendous variety of both styles of singing and styles of learning song. Kroodsma (1978) has pointed out that in most species only the males sing; however, depending on the species, the male may have a song repertoire of one song or a thousand; he may be an inferior or superior singer; he may learn new songs throughout his life or he may sensitive to song learning only during his first year. Nottebohm (1980) has tried to categorize these highly diverse birds into three manageable groups based upon their styles of vocal development. The categories are:

1. Birds which require no auditory feedback for the development of normal vocalizations and do not imitate external models (e.g., ringdoves).

2. Birds which require auditory feedback for normal development

but can produce a well-structured song in the absence of external models (e.g., canaries).

3. Birds in which the development of song is dependent on both the availability of auditory feedback and exposure to conspecific song models (e.g., chaffinch).

In this section I will attempt to apply the conditional probabilities model to each of these cases, which range over a full spectrum of genetic and environmental "direction" of development.

In the first case, birds that develop normal vocalizations independently of auditory feedback (hearing their own vocalizations) or external modelling (hearing the vocalizations of conspecifics) seem to depend on no necessary or requisite conditions for vocal development.[11] Species-specific vocalizations develop normally in ringdoves that are deafened or raised in auditory isolation. It appears that these vocalizations require the presence of only certain essential and emergent conditions during development. Probable essential conditions include oxygen, water, and nutrients, which are central to supporting the biochemical pathways of the organism; emergent conditions might include endogenous proprioceptive feedback from vocalizations or other function-structure relationships, although these have not been demonstrated experimentally. Birds in this first category lack vocal learning; Nottebohm (1980) offers the opinion that this is an evolutionarily primitive condition.

In the second category, birds require auditory feedback for vocal

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[11] This is not to exclude any possible conditions that might emerge from future experimental studies. For example, it is conceivable that a necessary condition for vocal development is appropriate hormone stimulation by the photoperiod or reproductive behavior. The manner in which these might act is outlined in the canary case.

development, but need not imitate an external model to produce a well-structured song. Let us more closely examine an example of this type of song development through a look at the male canary (Nottebohm, 1980). At about 40 days after hatching, the fledgling canary produces a rambling, low amplitude vocalization known as *subsong*. It is essentially noncommunicatory in function; Nottebohm (1980) hypothesizes that "during subsong the young bird is learning the auditory consequences of particular efferent commands." Subsong lasts for two to three weeks, whereupon it is transformed into *plastic song*. Nottebohm (1980) explains:

> As a canary sings, the units of repetition or "syllables" are rendered in quick succession, forming a "phrase." During plastic song, syllables and phrases are delivered in a variable manner, and this stage of song development lasts several months. A canary hatched in April or May sings the loud stereotyped song typical of adults by the following January, when 8 to 9 months old.

(See Figure 3 for an example of what syllables and phrases look like a sound spectrograph of canary song.) If the young canary is deafened before vocal learning takes place, it will produce an extremely abnormal song; however, if it is raised in auditory isolation, the canary can develop a well-structured song with stable phrasing. If external song models are available, though, the canary can and will imitate them.

The development of the neural areas that serve as "vocal control stations" in male canaries -- called HVc and RA[12] -- serves as an interesting parallel to song ontogeny. Although the brain of the

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[12] Abbreviations for the Hyperstriatum ventrale, pars caudale and the robust nucleus of the archistriatum of the brain.

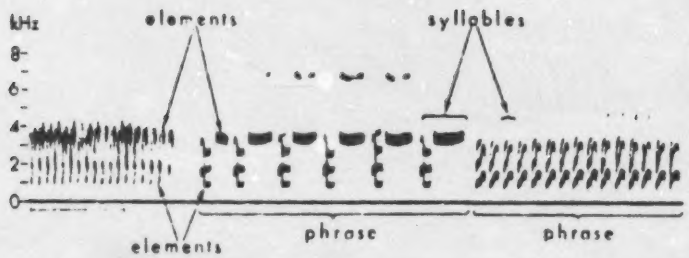

FIG. 3. Fragment of song of an intact adult male canary. This example includes three different phrases; each of the syllables in the first and second phrase is composed of two elements; syllables in the third phrase consist of a single element. Vertical and horizontal axes correspond, respectively, to frequency in kHz and time in seconds; horizontal bar indicates 0.5 sec. Second and third harmonics occur at twice and three times the frequency of the fundamental and should not be counted as different elements. From Nottebohm and Nottebohm (1976), reproduced with permission from *Journal of Comparative Physiology, A*.

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young canary has reached its adult weight by the fifteenth day after hatching, HVc is not yet recognizable through staining methods. From day 30 to day 60 after hatching, both HVc and RA show a marked growth spurt (roughly coinciding with the production of subsong); the rate of growth then slows down until adult sizes are attained at the age of one year. Both HVc and RA, as well as three other areas of the brain related to song production, are responsive to treatment with the hormone testosterone, which stimulates growth in these areas. Testosterone levels rise and fall in a seasonal manner in response to changes in photoperiod and the reproductive cycle. Nottebohm (1980) explains how depriving a canary of testosterone affects development:

> Male canaries castrated soon after hatching go through the early stages of song development. However, during the first year they fail to develop the loud, stable song typical of adults. Whereas intact first year canaries sing profusely from January to June, which coincides with the breeding season, early castrates of the same age remain silent.

The stimulative effects of testosterone can also be demonstrated on female canaries, which normally do not sing. Testosterone administration to females will induce singing (Nottebohm, 1980).

As a final complication to this example, canaries seasonally learn and forget their song repertoire (Nottebohm, 1981, in press). In the spring, when adult males are singing, HVc and RA are large. However, in the fall after the birds have been silent for several months, HVc and RA are 50% and 40% smaller, respectively. Upon the start of the next singing season, the two neural areas swell up again at the time when the males are developing a new song repertoire. This seasonal plasticity might be induced by the seasonal fluctuations in testosterone levels.

The four categories of conditions in the conditional probabilities model may help to sort out the different types of interactions going on in the development of canary song. Requisite conditions are, again, conditions that follow from other circumstances and are imposed externally, with a content that directly affects the expression of the end-state. Necessary conditions, however, are content-independent and result from circumstances more intrinsic to the organism than to the extra-organismic environment. It is not clear whether the auditory feedback from subsong production falls into the necessary or requisite category. If the canary could be "selectively deafened" to its own vocalizations, hearing some frequencies but not others, and was then found to produce an abnormal song (that perhaps might favor those frequencies heard), then auditory feedback would be said to be a requisite condition in the same way that the development of orientation selectivities in the visual system is dependendent on requisite conditions. If the canary produced a normal song, though, auditory feedback would be termed a necessary condition since the specific content of the auditory feedback did not affect the song produced. In either case, the feedback from subsong has interesting developmental consequences. Nottebohm (1980) suggests that the temporal overlap between subsong and the growth spurt in HVc and RA is not coincidental:

> An interesting possibility is that subsong experience may be made available at a time when it can be incorporated into the vocal control pathways: HVc and RA connectivity being established at that time may correspond, in some manner, to the auditory mapping of vocal tract function. Once this developmental stage is complete, then the bird is ready to imitate external models.

But this is a problem for the "development from" people.

A necessary condition for song development seems to be the action of testosterone on the vocal control stations of the brain. Testosterone may be stimulated by any of several means -- changes in photoperiod, reproductive behavior, or it may be applied exogenously -- all have the same effect. Seasonal fluctuations in testosterone levels may be necessary for the seasonal recurrence of neural and behavioral plasticity in the canary; the testosterone level does not, however, affect the "content" of the song.

Finally, a host of vaguely defined essential and emergent conditions must contribute to development, especially in the growth of brain areas HVc and RA. These factors include all the physical and endogenous functional events that spur development independently of sensory functional input. Again, it is unclear from experimental evidence which nonsensory factors are essential or how endogenously regulated function might contribute to song development.

In the third test case of the conditional probabilities model, the development of song is dependent on both auditory feedback and exposure to adult song models. Like canaries, male chaffinches progress through the developmental stages of soft, rambling subsong, increasing in complexity to become plastic song. Full song develops by the end of the first year, and is characterized by its stability and well-defined phrases. If a male chaffinch is raised in auditory isolation, it develops an aberrant song without phrasing or the typical complex ending; if the young bird is deafened at the age of three months, preventing auditory feedback before it has begun subsong, it will produce an extremely abnormal song -- in one bird, a continuous screech

(Nottebohm, 1970). Deafening the chaffinch after the establishment of full song, though, has no effect on its singing. The fledgling chaffinch normally hears adult chaffinch song during its first spring and summer. If the chaffinch is trapped in the summer and placed in auditory isolation, the following spring it will develop a close replica of the song it heard the previous year.

After the first year, each subsequent year the male chaffinch goes through the sequence of subsong, plastic song, and full song; however, unlike the canary, the chaffinch neither forgets his first-year song nor does he add any new songs to his repertoire. The song content remains stable after the first year of life, and the yearly recapitulation of the developmental sequence seems to be an artifact of seasonal fluctuations in testosterone levels (Nottebohm, 1970). It appears from the experimental evidence that song learning in the chaffinch takes place during a critical period in the first months of life, during which time the bird establishes a memory of an auditory "template" of the song, and then must convert this template into his own motor output. Both processes require an intact sense of hearing, and the former requires the presence of an external song model as well.[12]

Finally, although the vocal control areas of the brain are found in both its right and left hemispheres, chaffinch song production, like

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[12] Not just any song model will do -- the young chaffinch will learn only conspecific song. If presented with both chaffinch or song sparrow models, for example, the young bird will imitate only the chaffinch song. If he hears only song sparrow song early in life, he develops as though reared in auditory isolation.

that of canaries, is dominated by the left hemisphere. This phenomenon is akin to handedness in humans: the right-handed person favors his right hand for most tasks, but his left is by no means useless if unused. When the left hypoglossal nerve[13] of an adult chaffinch is cut, roughly 75% of syllables in his song are replaced by silent gaps or distorted sounds; however, the 25% of syllables controlled by the right side are produced normally. Early section of the left side in two week old chaffinches, though, leads to the development of normal song under the control of the right side. Nottebohm (1980) concludes:

> Thus, either syringeal half and its corresponding innervation can develop normal wild-type song, and copy a song model, or the two sides can collaborate in this task. In this respect the two sides are equipotential.

Although either left or right hypoglossals *can* develop control over song production, under normal circumstances only the left side actually *does*. The development of hemispheric dominance over song control may be in part testosterone-related, since female canaries treated with testosterone also develop left-side dominance.

In the chaffinch, both subsong and the presence of an external conspecific song model appear to be requisite conditions to song development. Both the model and the subsong itself seem to affect the content of the adult song. Even extremely abnormal song seems to reflect the bird's early auditory experience, since birds deafened at the age of three months tend to develop song elements reminiscent of the juvenile food-begging calls they produced as fledglings (Nottebohm,

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[13] The hypoglossal nerves are the nerves that innervate the two halves of the syrinx, which produce sound during expiration.

1970). Intact birds raised hearing a particular regional dialect of chaffinch song -- many dialects exist -- will closely imitate that dialect; thus the content of the early external model directly affects the eventual song content and structure.

As in the canary, chaffinch vocal development is testosterone-dependent. Testosterone stimulation (resulting from changes in the photoperiod, reproductive behavior, or exogenous application) is thus a necessary condition for song development. Also like the canary, there are probably some necessary conditions needed for the development of left-brain dominance over song control: these may include a combination of hormonal and auditory stimulation, perhaps resulting in an inhibitory effect of the left hemisphere over the right. (The processes controlling the development of hemispheric dominance are still poorly understood.) The pattern of testosterone stimulation may further affect the times at which requisite conditions for development -- external modelling and auditory feedback from song -- may have an effect. Chaffinches castrated before the age of six months do not sing -- they are not responsive to external auditory stimulation. However, a two-year-old castrate treated with testosterone well after the end of the normal critical period will develop a replica of the song which it hears during the hormone treatment. Thus it appears that the critical period for song learning (t_A and t_B in the conditional probabilities model) is testosterone-dependent (Nottebohm, 1980).

Finally, the essential and emergent conditions for song development in the male chaffinch can only be vaguely defined at this point, but are assuredly of great importance to development. Some endogenous

functional processes may especially affect the development of hemispheric dominance over song production, although such processes have yet to be demonstrated.

Advantages of the conditional probabilities model

These examples demonstrate that the conditional probabilities model can be usefully employed in a variety of developmental situations. The conditional probabilities model avaids some of the weaknesses of the genetic blueprint metaphor, while implicitly adopting one of the metaphor's strengths: that the genetic responses to an environment are given and strictly limit the course of development. However, this new approach explicitly presents the genetic processes as environment-expectant, giving a greater sense of the probabilistic dynamics of the process than the genetic blueprint model affords. Thus, the senses of essentialism and predeterminism that are often read into the blueprint approach are combatted from the start, in accordance with the "development from" perspective.

When applied to species-typical cases, the conditional probabilities model simplifies the treatment of expected environmental interactions by grouping them into categories based on the nature of their influence on development. Environmental factors are commonly seen as "strong" when they are requisite to development and shape the content of the outcome, and "weak" when they are nonsensory, essential factors which seem to merely facilitate development. As I will discuss later, the categories presented here may also aid in deciding how to classify

particular developmental pathways into the categories of "innate" or "learned" based on the strong/weak distinction, or whether indeed these classifcations are appropriate.

Development to endstates recognized by scientists as universal, normal, or species-typical can be well-handled through use of the conditional probabilities model.[14] It seems worth a short detour to explore these concepts of normal, natural, and universal courses of development upon which the "development to" approach is largely based, before discussing the categorization of environmental factors as strong or weak.

Normal, natural, and universal

Monod (1972) has pointed out that "...in science there is and will remain a Platonic element which could not be taken away without ruining it. Amidst the infinite diversity of singular phenomena, science can only look for invariants." It is the perception of affinities between creatures within a species that drives ethology, and of those between whole species that has spurred on taxonomy and evolutionary science. Yet, the decision of what constitutes an affinity or a universality within a species may cause problems. Kagan (1981) describes the hypothetical dilemma of biologists studying the embyogenesis of

[14] To study individual, unique courses of development, however, would require a more explicit description of the genetic character of the individual. In other words, rather that to assume a species-typical genome, as does the current model, one would have to include specific genetic conditions as well as environmental ones. For example, to apply the conditional probabilities model to severe mental retardation, an endstate not typical of human development, one might want to include a genetic condition such as having an extra chromosome, as occurs in Down's Syndrome.

the sea urchin:

> If the hypothetical biologists placed each of three sea urchin eggs in three growth media differing in acidity and temperature and discovered three different courses of morphologic development, they might not conclude that there was a universal developmental course with variations depending on local conditions. Rather, the biologists might decide that there were different ontogenies depending on the conditions of growth. That conclusion would irritate some traditional biologists, who would reply that there is a universal sea urchin and an optimal ontogeny; namely, the potential contained in the genome. It is assumed that the universal form is the one that occurs most often in nature; the others are variations on that ideal.

The problem is, how can the "infinite diversity of singular phenomena" that develop in response to local conditions be marshalled into a scheme of universals? Kagan (1981) points out that some would have the most frequently occurring form in nature serve as the universal. But does this form more closely represent the "potential contained in the genome" than any other? The answer from the "development from" perspective must be no -- developmental outcomes do not lie latent in the genome, but are constructed through its interaction with an environment. Thus, the modal form in nature is no more than a result of the genome interacting with the modal environment. Neither developmental course of the long-billed wren is more universal than the other -- recall that early born males develop song during the first summer, while late-born wrens postpone song-learning until the following spring -- although the majority develop via the former pathway.

Kagan (1981) argues that in spite of this diversity of particular ontogenies, we must still develop a concept of universals, for "although performances may vary across contexts, as chemical reactions

vary with acidity, pressure, and temperature, the potential for a particular performance is universal." Kagan argues that a more abstract, philosophical definition of universals as *concepts* which "consist of the characteristics common to a variety of particulars" proves a better construct than that of universals as modal forms in nature, which are themselves particular forms. He goes on to cite one example of a "conceptual," rather than a "particular," approach to the development of universal competencies:

> Between about 7 and 20 months of age, human infants are particularly vulnerable to inhibition and distress when faced with a discrepant event that cannot be assimilated. Examples include unfamiliar adults, children, or separation from a caretaker. The specific events that generate the mood of uncertainty and the ages at which the apprehension appears and declines will depend on local conditions. Thus the statement that stranger and separation anxiety are universals perhaps should be replaced with the following proposition: human infants between 7 and 20 months of age will show a low threshold for uncertainty to certain classes of discrepant events but the specific event that provokes fear will depend on the local conditions of growth. A Fiji 12-month-old is likely to show extreme fear to a small doll because it is extremely discrepant from his or her experience; such behavior is rare among American infants. (Kagan, 1981)

A conceptual approach to universals thus relies on abstract categories to encompass many possible particular outcomes. Language, song, and distress, for example, may be more appropriate terms for universals than are Chinese, Berkeley white-crowned sparrow dialect, and stranger anxiety.

However, a question linked to this subject is just how universal are these universals? Even these developmental outcomes may be obstructed by a radical change in the normative environment. Severely abused and isolated children may fail to develop language abilities --

clearly, even the development of universals hinges on environmental factors present in the range of normal, expected environments. "Universal" need not imply "inevitable"; the subject of evitability in development is best discussed under a separate heading.

Innate and experiential -- the semantics of nature-nurture

Any discussion of how development proceeds toward some species-typical endstate is fraught with terms like learned, inherited, experiential, innate -- terms which are easily misused or misunderstood. What each has in common with the others is that it is commonly used to denote in some way the relative strength of the genes and the environment in directing the organism toward some developmental outcome. All mean different things to different people, and the oversight of failing to define one's terminology has surely charged many a political debate in the history of the nature-nurture question. "Nature" and "nurture" are themselves awkward terms, not at all synonymous with genetic and environmental, as I use them, or with any of the above terms. This section is an attempt to sort out the meanings of some of these words, choose those that appear most useful and least charged, and define them carefully.

The term "inherited," for example, has been absolutely central to the controversy over the roles of the genes and the environment in the development of intelligence. When a geneticist speaks of a trait or a character as inherited, he means that it is possible to predict the distribution of the character in a population living

in a certain environment, given that he knows the distribution of the character in the parent population and the pattern of mating in that population. Put differently,

> ...a character may be said to be "inherited"...if the variation of this character from individual to individual can be shown to arise from differences in the genetic constitution...of different animals, rather than from differences in the kind of environment in which they have been reared.... (Lehrman, 1970)

Geneticists are not inferring, though, that the developmental processes in the ontogeny of the character are independent of the environment, or that the character might not be radically altered by rearing in an environment other than the one tested. However, a second, separate meaning ascribed to the word inherited by non-geneticists is that of *developmental fixity* -- "that the organism is impervious to environmental effects during development, and so it *must* develop characteristics that are preorganized 'in the genes,' regardless of the environment in which it is reared" (Lehrman, 1970). This is contrary to the geneticist's use of the term. It should be clear that, if one's intent is scientific accuracy in discussing the nature-nurture question, one must explicitly define and delineate one's use of the term inherited if one uses it. It is useful and productive only when it is

> ...recognized that the observations that justified the conclusion that the difference between the two animals was a genetic difference do not necessarily imply anything, one way *or* the other, about the extent to which the development of the character concerned is, in either animal, influencible by changes in the environment. (Lehrman, 1970)

The *same* genotype may, during development in a different environment, produce a different phenotype -- yet in each environment, the popu-

lation shows a high heritability of the trait. For example, a wide variety of genetic mutations cause variations in the wing structure of the common fly *Drosophila melanogaster*; the mutations also affect the fly's ability to fly. Different flies that carry the same genetic mutation will be able to fly normally only when they are raised in an environment at a moderate temperature. Flies with the same genotype raised above this temperature range are able to fly only weakly, and flies raised in colder environments not at all (Harnly, 1941). In this vein, Lewontin (1974) has pointed out that "a trait can have a heritability of 1.0 in a population at some time, yet could be completely altered in the future by a simple environmental change." In any discussion of heritability and genetics, it becomes crucial to distinguish between the technical and everyday meanings of the term inherited.

On the other side of the nature-nurture coin, another (less politically charged) semantic confusion arises over the terms "experience" and "learning." Often the two are equated (e.g., Lorenz, 1965), yet modifications of the visual nervous system, for example, are effected by a complex physiological interaction between the organism and its environment. Such experience-based modifications are not what we usually mean by "learning." Although learning is certainly one form of experience, the distinction between it and other forms may be murky. Furthermore, some may view experiential events that are furthest away from learning on a spectrum as more a part of nature than nurture. For example, autogenous function or hormonal changes due to environmental events such as a seasonally fluctuating photo-

period may be viewed as nature variables since the organism is not taught, does not imitate, or otherwise learn during the development facilitated by these events. It is not avoid this confusion that I have chosen to word my arguments in terms of genetic and environmental influences, which can be more strictly delineated than natural or nurtured. "Genetic" and "environmental," though, give no clue to the "strength" of influence over the outcome -- what we are looking for in this section are terms that will offer some indication of how potentially disruptible the process leading to some outcome is.[15]

The range of environmental conditions and effects outlined in the conditional probabilities model implies that there can be no simple dichotomy in the extent of genetic or environmental control over development -- no structure results solely from one or the other, and there are several possible modes of environmental action. Clearly there must exist some sort of spectrum of degrees of control. I have chosen to use the terms innate and experiential to roughly describe the two ends of this spectrum, and to state explicitly that a developmental event need not, and often will not, fit neatly into either of these two categories. *Innate* developments are here defined as those which most readily approximate a continuous series model of development, with the genome constituting the source of the impetus

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[15] Strictly speaking, the idea that either a genetic or an environmental factor can be strong or weak in and of itself is an inappropriate one. Even at the level of essential conditions, the gene and the cytoplasmic environment *jointly* determine the functional characteristics of the enzymes and proteins that do the work of development. It is useful, though, in considering the "development to" perspective, to have some idea of to what extent environmental factors determine the content of the endstate, or to what extent this development can be disrupted.

behind development. Although the environmental interactions are real and must occur, we are sufficiently confident in their presence as to take them for granted (Scheffler, 1980). *Experientially-based* development, on the other hand, can be described only through the use of a model that emphasizes experience with relevant environmental conditions. For example, in the birdsong cases, vocal development in ringdoves could be termed innate since it proceeds independently of auditory experience; chaffinch song development is more experiential, though, since it depends on both auditory feedback and learning from an external model, and it is not at all difficult to imagine a situation in which these factors could be disrupted. Universals in development may be innate or experientially-based, according to these definitions.

Much of what determines whether a developmental pathway is more aptly classified as innate or experiential has depended on the state of the science that studies it. The recognition of the species-specific maternal call by a newborn duckling was termed innate until it was found that the embryological experience of the duckling hearing its own high frequency vocalizations clearly contributes to its recognition at hatching of the appropriate call, at which point the development was termed experiential (Gottlieb, 1976). If innate can never mean "developmentally fixed" or predetermined, how much experiential input should one allow for something to be termed innate? In the present system, one can safely classify the duckling's development on the innate side of the spectrum: the embyological functioning and feedback can be counted on to occur, unless a scientist interferes with the

embryological duckling's vocal production. Because there is normally very little chance of disruption of this process, it may approximate a continuous series. Still, it must be emphasized again that a continuum is at work here. Because it is more conceivable that an extraorganismic, postnatal event -- like a long-billed wren hearing adult song -- might be disrupted than a more endogenous event, the former is more easily thought of as experiential. Innate and experiential are, in the long run, terms that are used for convenience, not for precision, in talking about development.

SUMMARY AND IMPLICATIONS FOR POTENTIAL

This attempt at a theoretical synthesis of the "development from" and "development to" perspectives in biology has offered the joint notions of probabilistic epigenesis and conditional probabilities in species-typical development. While not attributing to the genome a knowledge of or the information about developmental outcomes, it allows one to talk about endstates in the context of specific, expected environmental conditions. The environmental conditions fall into four categories: essential, emergent, necessary, and requisite. Outcomes that depend only on the interaction of the genome with more dependable, essential and emergent conditions tend to be thought of as innate (e.g., the pecking of a newborn chick). Outcomes that depend strongly on necessary and requisite conditions as well as the former two types tend to be thought of as more experientially-based (e.g., the development of chaffinch song). Yet, in each and every case, both genome and environment limit and contribute to the probability of each possible outcome.

I have argued in this paper that potential cannot, as some biologists would state or imply, lie latent in the genome. The genome can have no knowledge of an optimal ontogeny or a modal endstate -- the information for development must lie in the interaction between the genome and the environment. Once the observer has identified some of the characteristics of both, however well he can, these developmental paths and outcomes can be predicted on the basis of conditional probabilities which take both into account.

Given an organism in a particular environment, the number of potential paths of development is large but finite. Probabilistic epigenesis implies that, with development through the modification or transformation of existing structures, some outcomes that were potentials for the newborn are no longer open to, say, the teenager. Kuo (1970) writes:

> At the beginning of life the individual possesses an enormous range of behavioral potentials....As ontogenesis proceeds, new behavior patterns are actualized out of potential patterns and added to the existing *repertoire* at the same time ontogenetic processes set a limit to the actualization of certain other patterns, either as a result of the gradual loss of plasticity of the structures and function of the organs of the organism, or because of the incompatibility of such potential patterns with the actualized patterns.

The conditional probability approach to development also implies that the number of potentials becomes limited with time: if the organism passes t_A and t_B without encountering A or B (and if an alternative pathway to E_s springs up, hinging on C at t_C, but C never occurs), E_s will never develop.

Finally, given the limitation of realizable environments in our world, some developmental pathways are weighted more heavily (are more probable) than others. In other words, the probability that A and B will be met, and the conditional probability itself, are very high. These may be termed universals in development, and are, according to Kagan (1981), best thought of as conceptual descriptions of sets of particular outcomes, rather than as the modal forms in nature.

Thus, the following summary points outlining the relationship between the study of potential and this dual approach to developmental

theory can be offered:

1. Given a particular organism in a particular environment, the number of potential paths of development is large but finite due to both genetic and environmental constraints.
2. Given a particular organism is an infinite number of environments, the number of potential paths of development may be infinite. However, a given imaginable potential may not be realizable in any of the possible worlds due to the limits placed on development by the genome.
3. Given the organism in a particular environment, some developmental paths may approximate a continuous series rather than an interactive model, because the observer can count on the interactive factors. These are termed innate.
4. In a particular situation, an outcome that is highly probable or even universal may be so because the genetic factors maintain a large amount of "control" -- only radical events (like severe malnutrition or embryologic paralysis) will alter the developmental path; alternatively, with other universal outcomes, environmental influences may exert the greater control (e.g., all male chaffinches learn a regional dialect).

One can only conclude that potential paths or steps of development can only be predicted from knowledge about the genome *and* the environment, and that predictions about the probability of any particular developmental path being followed can be made only in conjunction with knowledge about the outcomes of development of a variety of genotypes in

in a variety of environments. This view of species-typical development accommodates both facets of a developmental synthesis: development to an endstate as a result of a high probability that a conditional probability will be met, that expected environmental events will indeed be encountered, and development from any state based on a complex interaction between a genome and a particular, local environment. Clearly, developmental outcomes are latent in neither the genome nor the environment, but are constructed and limited by both.

REFERENCES

Bekoff, M. and M.W. Fox (1972) Postnatal neural ontogeny: Environment-dependent and/or environment-expectant? *Devel. Psychobio. 5,* 323-341.

Fodor, J.A. (1980a) Methodological solipsism considered as a research strategy in cognitive psychology. *The Behavioral and Brain Sciences 3,* 63-109.

Fodor, J.A. (1980b) *The Language of Thought.* Cambridge: Harvard University Press.

Galambos, R. (1970) Prefatory remarks on the determinants of neural and behavioral plasticity. In F.O. Schmitt (Ed.) *The Neurosciences Second Study Program.* New York: The Rockefeller University Press.

Galambos, R. and S.A. Hillyard (1970) Determinants of neural and behavioral plasticity: An overview. In F.O. Schmitt (Ed.) *The Neurosciences Second Study Program.* New York: The Rockefeller University Press.

Gottlieb, G. (1970) Conceptions of prenatal behavior. In L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt (Eds.) *Development and Evolution of Behavior.* San Francisco: W.H. Freeman and Company.

Gottlieb, G. (1976) Conceptions of prenatal development: Behavioral embryology. *Psych. Rev. 83,* 215-234.

Harnly, M.H. (1941) Flight capacity in relation to phenotypic and genotypic variations in the wings of *Drosophila melanogaster. J. Exp. Zool. 88,* 263-273.

Kagan, J. (1981) Universals in human development. In R.H. Munroe, R.L. Munroe and B.B. Whiting (Eds.) *Handbook of Cross-Cultural Human Development.* New York: Garland STPM Press.

Kagan, J., R.B. Kearsley and P.R. Zelazo (1978) *Infancy: Its Place in Human Development.* Cambridge: Harvard University Press.

Kitchener, R.F. (1978) Epigenesis: The role of biological models in developmental psychology. *Hum. Dev. 21,* 141-160.

Kroodsma, D.E. (1978) Aspects of learning in the ontogeny of bird song: Where, from whom, when, how many, which, and how accurately? In G. Burghardt and M. Bekoff (Eds.) *Ontogeny of behavior.* New York: Garland Publishing.

Kroodsma, D.E. and R. Pickert (1980) Environmentally dependent sensitive periods for avian vocal learning. *Nature 288,* 477-479.

Kuo, Z.-Y. (1970) The need for coordinated efforts in developmental studies. In L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt (Eds.) *Development and Evolution of Behavior*. San Francisco: W.H. Freeman and Company.

Lehrman, D.S. (1970) Semantic and conceptual issues in the nature-nurture problem. In L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt (Eds.) *Development and Evolution of Behavior*. San Francisco: W.H. Freeman and Company.

Lerner, R.M. (1978) Nature, nurture, and dynamic interactionism. *Hum. Dev. 21,* 1-20.

LeVay, S., T.N. Wiesel and D.H. Hubel (1980) The development of ocular dominance columns in normal and visually deprived monkeys. *J. Comp. Neurol. 191,* 1-51.

Lewontin, R. (1974)

Lorenz, K.Z. (1965) *Evolution and the Modification of Behavior*. Chicago: University of Chicago Press.

Monod, J. (1972) *Chance and Ne essity*. New York: Vintage Books.

Nottebohm, F. (1970) Ontogeny of bird song. *Science 167,* 950-956.

Nottebohm, F. (1980) Brain pathways for vocal learning in birds: A review of the first 10 years. *Prog. in Psychobiol. Physiol. Psych. 9,* 85-124.

Nottebohm, F. (1981) Laterality, seasons, and space govern the learning of a motor skill. Submitted to *Trends in Neuroscience*.

Scheffler, I. (1980) Pondering potentiality. Unpublished manuscript for the Project on Human Potential, Harvard University Graduate School of Education, December 18, 1980.

Weiss, P.A. (1970) Neural development in biological perspective. In F.O. Schmitt (Ed.) *The Neurosciences Second Study Program*. New York: The Rockefeller University Press.

Wilson, E.O. (1979) *On Human Nature*. Cambridge: Harvard University Press.